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柳兰广布种在中国的变异式样及其分类学

陈 家 瑞 彼得 · 霍克 彼得 · 雷文 (中国科学院植物研究所,北京) (美国密苏里植物园,圣路易斯)

摘要 本文着重对分布于中国的柳兰 Epilobium angustifolium L. 进行了细胞学、形态学、花粉学及地理学研究,发现有二倍体 (n = 18) 和四倍体 (n = 36) 及其相关形态学性状和分布区,认为把不同种宗处理作二个亚种——柳兰 subsp. angustifolium (二倍体)和毛脉柳兰 subsp. circumvagum Mosquin (多倍体)是适宜的。不同倍性柳兰的花粉直径、花粉孔数、叶背面中脉毛被及叶片宽度不同 (Mosquin, 1966),我们还观察到叶片基部形状、叶缘、花序轴毛被等也是区别不同倍性柳兰的好性状。柳兰的形态学差异是染色体倍性决定的,这是以多倍化形式进化的又一例证。本文报道了 11 号柳兰样品染色体计数,其中 6 号为二倍体,5 号为四倍体,后者在亚洲为首次报道。柳兰的细胞地理学资料表明:柳兰可能是温带起源,在喜马拉雅地区柳兰可能是从东西不同方向分别进入这个地区的。

关键词 中国;柳兰;复合种;变异式样;细胞学;分类学;地理学

前 言

柳兰 Epilobium angustifolium L. 是一个复合种,广布于北半球温带。 自 1753 年 C. Linnaeus 记载了这种植物以来,它的名称稳定,虽然发表过少数种下等级名称,但一直未得到承认。 然而,近来发现了柳兰存在着三个不同倍性种宗: n = 18 (二倍体)、n = 36 (四倍体)和 n = 54 (六倍体) (Mulligan 1957; Löve and Löve 1961; Mosquin 1963 a & b, 1966; Raven and Moore 1964),从而对柳兰过去分类学结论产生了疑问,是否要对每个倍性种宗定为不同的种? Mosquin (1966a) 发现柳兰多倍性具有很高频率的链和环式染色体构型,他通过杂交试验,认为四倍体与六倍体植物是同源多倍体;他还认为不同倍性的柳兰形态学上的变异基本上是量变的性质。因此,他把柳兰正式分为二个亚种: 柳兰 Subsp. angustifolium (n = 18) 和毛脉柳兰 Subsp. circumvagum Mosquin (n = 36,54)。 然而,他的细胞学研究材料多取自美洲,自欧亚大陆的仅有英国1号(n = 18) 和日本1号(n = 54)。 他承认这两个亚种在北美易分辨,重叠区较小,而在亚洲的却复杂得多,很难做出正确的判断。 以同样理由, Raven (1968, 1972), Hoch & Raven (1981) 和中国植物学家[1-5]在研究亚洲的柳兰时仍作单型种处理。

本文作者在 1981—1986 年先后在美国和中国对柳兰又进行了较深人的研究,普遍检查了大量采自中国及邻近地区的约 1500 号腊叶标本,结合温室栽培观察动态性状 (dynamic character) 和开花习性,对不同类型进行细胞学与花粉学观察,还在中国西南部、华北和西北部分地区进行了野外工作。目的在于运用综合分析方法,弄清柳兰在中国及其邻近地区的变异式样,以解决这种植物多年存在的分类学与地理学问题,借以探讨广布

种的生物学与分类学。

观察结果

繁育习性 柳兰是一种雄蕊先熟异花受粉植物,但自花可亲合。花药开花时成熟,花粉以单个形式散发,花粉之间被粘丝粘成团,然而这时的柱头仍关闭着,花柱强烈下弯远离花药,开花二、三天后,花柱微伸长并变直立,柱头裂片展开,这时花柱基部的蜜腺开始分泌蜜,吸引昆虫传粉,传粉阶段一般需要 4—6 天。此外,有时可借助于风传粉。在恶劣气候下,花粉可育率很低,如毛脉柳兰 Subsp. circumvagum 采自四川峨眉山北麓海拔 550m的陈嵘 7133(NAS) 和理县海拔 4300m 的何获平 46527(SZ) 的花粉败育率均达 91%。

柳兰的传布方式同柳叶菜属其他植物一样,主要靠风力传布有种缨的种子。然而柳兰组的种同柳叶菜组的种则不同,蒴果大 2-4 倍,每一果实的种子有 300—500 粒,要 多 1—2 倍,种缨长 13—17mm。柳兰的地下茎与根系远较本属的其他种植物的发达,在地下 5—20cm 深处盘根错结,从地下茎长出根出条进行无性繁殖,常成片生长。

细胞学 我们对采自中国的 11 号柳兰进行了细胞学观察 (见表 1),这同 Mosquin (1963a) 观察到的其他地方柳兰的结果一致,至少存在有 2 个染色体类型种宗,n=18 (二倍体)和 n=36 (四倍体),但尚未发现六倍体 n=54。

表 1 柳兰染色体计数

Table 1 Chromosome counts for Exilobium angustifolium

凭证标本及其保存处 Collection (herbarium preserved voucher)	采集 地 Locality	配子体染色体数 Gametic chromo- some number (n)
李书纂等 (S. X. Li et al.) Aug. 1982, s. n. (MO)	吉林,长白山 Jilin, Mt. Changbai	18
H. J. Meng 75 (NMU)	内蒙古,兴安盟 Nei Monggol, Hinggan Meng	18
张振万等[Z. W. Zhang et al. 4443 (XJBI)]	新疆,阿勒泰 Xinjiang, Altay	18
李恒 (H. Li)Aug. 31, 1981, s. n.(MO)	四川,巴塘 Sichuan, Batang	18
陈伟烈及陈家瑞 [W. L. Chen & C. J. Chen 6305, (PE)]	四川,康定沙德 Sichuan, Kangding	18
陈伟烈及陈家瑞 (W. L. Chen & C. J. Chen 7977, PE)	四川,阿坝 Sichuan, Aba	18
Y. Z. Liu Aug. 1981, s. n. (NMU)	内蒙古,呼伦贝尔盟 Nei Monggol, Hulun Buir Meng	36
神农架队 [Shenlongjia Bot. Exped. 22844 (PE)]	湖北,神农架 Hubei, Shenlongjia	36
陈伟烈及陈家瑞 [W. L. Chen & C. J. Chen 8807 (PE)]	甘肃,文县 Gansu, Wen Xian	36
陈伟烈及陈家瑞[W. L. Chen & C. J. Chen 8450 (PE)]	四川,南坪 Sichuan, Nanping	36
陈伟烈及陈家瑞[W. L. Chen & C. J. Chen 7981 (PE)]	四川,阿坝 Sichuan, Aba	36

减数分裂观察,将花蕾用卡诺 I 固定液固定一天,把材料换入 70% 乙醇中保存于冰箱内(野外固定的材料,制片前还需重新固定),压片前用 1mol/L 盐酸在 60℃ 温箱中水解 2 分钟,或用 1:1 的浓盐酸与乙醇室温下水解 1—2 分钟,用醋酸洋红染色压片观察。

形态学 我们对柳兰的约一百个性状进行了观察,发现下述九个性状具有分类学意

表 2 柳兰的花粉直径、孔敷和败育率

Table 2 Diameter, pores and infertile percentage of pollen in subsp. angustifolium

凭证标本和存放地 Specimen (herbatium)	jàc 地 Locality	2-porate (%)	3-porate (%)	四孔 4-porate (%)	五孔 5-porate (%)	政育奉* Infertile (%)	直径 Diameter (µm)
王战 Z. Wang 897 (IFP)	内蒙古-滿對里 Nei Monggol, Manzhouli	1	97	7	0	κ,	57.5
这位场等 T. N. Lion et al. 7321 (PE)	黑龙江,尚志 Heilongjiang, Shangzhi	0	95	IO.	0	4	65.1
刘慎鸿等 T. N.Liou et al. 7204 (PE)	黑龙江,尚志 Heilongjiang, Shangzhi	0	100	0	0	2	58.9
影番祥等 Z. X. Peng et al. 282 (LZU)	甘肃,玛曲 Gansu, Maqu	0	98	2	0	21	65.1
张玉良 Y. L. Chang 546 (PE)	吉林,抚松 Jilin, Fusong		9.6	4	0	9	67.5
小五合山以 Xiaowutai Shan Exp. 74078 (PE)	河北,小五台山 Hebei, Mt. Xiaowutai	0	100	0	0	25	79.7
Y. Yabe July 3, 1906, s. n. (PE)	河北,小五台山 Hebei, Mt. Xiaowutai	0	100	0	0	9	64.0
账振万等 Z. W. Zhang et al. 3509 (XJBI)	新疆,巩留 Xinjiang, Gongliu	0	100	0	0	20	74.8
刘国勉 G. J. Liu 685 (XJBI)	新疆,阿尔泰山 Xinjiang, Altay	0	100	0	0	10	70.7
周太炎 T. Y. Chou 652073 (XJBI)	新疆,阿尔泰山 Xinjiang, Altay	0	86	2	0	ın	75.1
周太炎 T. Y. Chou 651180 (NAS)	新疆,天池 Xinjiang, Tianchi	0	100	0	0	mi	71.6
张泽荣及周洪信 Z. Y. Zhang & H. F. Zhon 23763 (SZ)	四川,剛经寺 Sichuan, Shuajingsi	2	86	0	0	oc	66.4
张秀实 S. S.Chang 6172 (SZ)	四川小小金 Sichuan, Xiaojin, 3500m	0	100	0	0	oc	69.1
张秀敦 S. S. Chang 6050 (SZ)	四川小小金 Sichuan, Xiaojin, 3300m	0	100	0	0	26	1.69
张秀奖 S. S. Chang 5970 (SZ)	四川,小金 Sichuan, Xiaojin, 2900m	0	100	0	0	10	74.3
武素功 S. K. Wu 7(MO)	四川, 粗城 Sichuan, Daucheng, 4400m	0	66	=	0	13	65,1
杨亚宾 Y. B. Yang 104 (CDBI)	四川,城周山 Sichuan, Mt. Emei, 3135m	0	88	12	0	22	75.3
方文培 W. P. Fang 20434 (PE)	四川。峨眉山 Sichuan, Mt. Emei, 3000m	0	100	0	0	16	67.7
Y. H. Dao 50442 (SZ)	四川,城眉山 Sichuan, Mt. Emei, 2950m	0	66	-	0	14	4.69
俞蘅浚 T. T. Yu 11961 (GH)	云南,中甸 Yunnan, Zhongdian	0	100	0	0	-	62.1
平均 Average		0.25	98.35	1.4	0	10.55	68.43

* 花粉败育率用孔雀绿-酸性品红-桔红G试剂,以不着红色花粉粒的百分比计算 (Alexander, 1969).

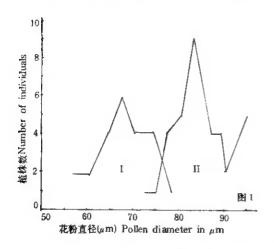
表 3 毛脉搏兰的花粉直径、孔敷和败育率

Table 3. Diameter, pores and infertile percentage of pollen in subsp. circumsugum

凭证标本和存放地 Specimen (herbarium)	产 地 Locality	二孔 2-porate (%)	三孔 3-porate (%)	四孔 4-porate (%)	五孔 5-porate (%)	三孔 四孔 五孔 败育率 3-porate 4-porate 5-porate Infertile (%) (%) (%)	直径 Diameter (µm)
底立二組 Yanbian Group 2 924(PE) 正达二組 Yanbian Group 2 924(PE) 木北斯大 NE Teachers' Univ. 399(NETU) 小五台山队 Xiawutai Exped. 274(PE) Y. Yabe July 3, 1906, s. n.(B) Y. Yabe July 3, 1906, s. n.(B) Y. C. Liu 2303(NY) 地南京 C. G. Yang 748(PE) 山京以 Shangdong Exped. 3142(PE) 東西東京等 C. G. Yaui et al. 80044(PE) 東西東京等 C. W. Liu 2084(HNWP) 華高森等 H. P. Tsui et al. 80044(PE) 東西東京 Z. S. Chang et al. 5995(SZ) 展示表文 S. Chang et al. 5995(SZ) 展示表文 S. Chang et al. 5995(SZ) 展示表文 S. Chang et al. 5995(SZ) R. Yang 23439(P) S. H. Wu 19(SZ) 参大塔 W. P. Fang 2822(E) S. L. Yang 57442(SZ) S. Tu 49923(SZ) S. Tu 49923(SZ) S. Tu 49923(SZ) S. W. Liu T. Yu 3432(PE) 四川经済権物队 Sichuan Econ. Pl. Exp. 1993(PE) 四川経済権物队 Sichuan Econ. Pl. Exp. 1993(PE) 四川経済権物队 Sichuan Econ. Pl. Exp. 1993(PE) 西川経済権物、Nicang Exped. 1867(HNWP) 西山隆 Jun. 1906, s. n.(E) 西瀬良 Xizang Exped. 1867(HNWP)	黑龙江,东部 E Helongjian, Djalantum 吉林,合隆 Jilin, He long 古本,合在 Jilin, He long 古本,合在 Jilin, Mt. Changbai 尚北,小五台山 Hebei, Mt. Xiaowutai 尚北,小五台山 Hebei, Mt. Xiaowutai 尚北,小五台山 Hebei, Mt. Xiaowutai 尚北,亦在台山 Hebei, Mt. Xiaowutai 尚北,亦在台山 Hebei, Mt. Xiaowutai 尚北,亦在台山 Hebei, Mt. Xiaowutai 尚北,亦在台山 Bhangdong, Mt. Kunyu 陳茂,是由山 Shangin, Mt. Taibai 青海,建中 Qinghai, Huangzhong 青海,建中 Qinghai, Huangzhong 青海,建中 Qinghai, Huangzhong 青海,建中 Qinghai, Huangzhong 清海,建中 Qinghai, Huangzhong 清海,建中 Qinghai, Huangzhong 尚末,神衣架 Hubei, Shennongjia 200m四川,冰在 Sichuan, Wushan 四川,小金 Sichuan, Mt. Emei, 3000m四川,城昌山 Sichuan, Mt. Emei, 2200m四川,城昌山 Sichuan, Mt. Emei, 2200m四川,城昌山 Sichuan, Mt. Emei, 2200m四川,城昌山北麓 Sichuan, Mt. Emei, 550m四川,城昌山北麓 Sichuan, Leibou 四川,赛应 Sichuan, Lainguan 四川,赛应 Sichuan, Leibuu 云南,碧江 Yunnan, Lijiang 云南,碧江 Yunnan, Lijiang 云南,瑶水 Yizang (Tibet), Yadong	0-050%,,,0000000000000000000000000000000	53 447 747 833 111 100 100 100 100 100 100 1	4751818254214	001000000000000000000000000000000000000	01 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	80000000000000000000000000000000000000
平均 Average		0.25	75.2	23.11	1.44	14.35	85.68

义。

1. 花粉 我们对采自中国的 57 号标本柳兰花粉进行了显微观察测量(表2-3),发现不同倍性的花粉大小明显不同,在他们的曲线图上出现二个高峰(图 1);其荫发孔的数目也随倍性提高而增多,这与 Stebbins (1950) 关于多体论述相吻合。二倍体柳兰的花粉直径平均为 68.43(57.5-79.7) μm。 其孔数: 3 孔为 98.35%,4 孔为 1.4%,2 孔为0.25%,败育率为 10.55%。而四倍体柳兰的花粉直径平均为 85.68(72.4-94.8) μm。 其孔数: 3 孔为 75.2%,4 孔为 23.11%,5 孔为 1.44%,2 孔为 0.25%,败育率为 14.35%。花粉的败育率与染色体倍性(除奇数者外)似无重要关系,可能主要受杂交与生长环境的影响,如采自北京的 T. F. King 364(PE) 二倍体柳兰花粉败育率为 25%,采自西藏樟木的张永田与朗楷永 651(PE) 毛脉柳兰花粉完全败育,很可能是一个杂交后代不育个体。而采自四川峨眉山海拔 550m 亚热带地带的陈嵘 7133(NAS)四倍体柳兰花粉败育率达 91%。不同倍性柳兰的花粉学性状与地理分布存在着相关性。图 3 清楚地显示出:花粉较大、孔数多的四倍体毛脉柳兰分布纬度较低、海拔较低,即综合地理单位较少(详见下节讨论);而花粉较小、孔数较少的二倍体柳兰分布纬度则较高、海拔较高,综合地理单位也较多。



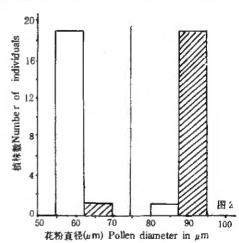


图 1 柳兰不同倍性种宗花粉直径曲线图

Fig. 1 Curves for pollen diameters of diploids and tetraploids in E. angusufolium, showing two curvilineal peaks.

I. 二倍体 Diploid; II. 四倍体 Tetraploid。 花粉数据为 20 粒平均数 X of 20 grains。

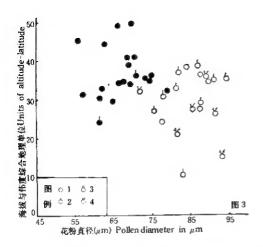
图 2 柳兰不同亚种的叶中脉背面毛被与花粉直径相关性

Fig. 2. Diagram showing correlation between the pollen size and the pubescence of an abaxial leaf midrib in different subspecies of E. angustifolium.

白柱=叶中脉背面无毛; 斜线柱=叶中脉背面被毛。

open column = abaxial leaf midrib glabrous; slant column = abaxial leaf midrib pubescent. 柳兰 Subsp. angustifolium, 二倍体 Diploid, 花粉直径 pollen diameter (48.6—) 57.5—79.7 μm; 毛脉柳兰 Subsp. circuvagum, 四倍体 Tetraploid, 花粉直径 pollen diameter 72.4—94.8(—108)μm。

2. 中脉背面与花序轴的毛被 图 2 表明柳兰花粉 直径 小的 [(48.6)57.5—79.7 μm] 二倍体类群,其叶中脉背面及花序轴无毛,仅极个别有少量的毛;花粉直径大的 [72.4—



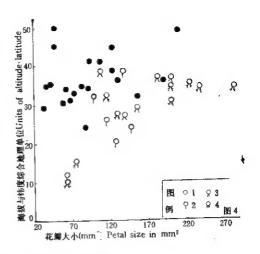


图 3 柳兰不同亚种的花粉直径、孔数与地理分布关系

Fig. 3 Scatter diagram, showing correlation between pollen charaters and geography in different subspecies of E. angustifolium.

黑点 solid circle = 柳兰 Subsp. angustifolium; 白圈 open circle =毛脉柳兰 Subsp. circumvagum. 1—4.200 粒花粉中含 4—5 孔的百分率(%) of 4—5-pored pollen of 200 grains:
1. 0—5%; 2. 6—30%; 3. 31—50%; 4. >50%.

图 4 柳兰不同亚种的叶中脉背面被毛与花瓣大小同地理分布关系 Between the morphology of both the leaf pubescence and petal size and geography in different subspecies. of E. angustifolium.

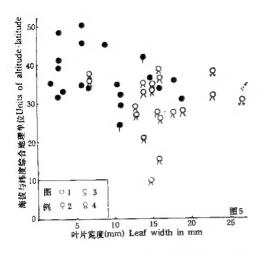
黑点 solid circle = 柳兰 Subsp. angustifolium; 白圈 open circle = 毛脉柳兰 Subsp. circumvagum. 1—4.叶中脉背面每 mm² 被毛数 pubescence on 1mm² of abaxial leaf midrib: I. glabrous;

2. 1—50 trichomes; 3. 51—100 trichomes; 4. >100 trichomes.

94.8(—108)µm] 四倍体毛脉柳兰则或多或少被毛(图 4)。 这一性状与花粉直径存在着相关性。

- 3.叶片 柳兰的叶片基部,二倍体的钝形或圆形,四倍体的楔形。叶片边缘,二倍体的常全缘,多少反卷,而四倍体的近平坦,或多或少有细点状齿。叶片宽度,二倍体的普遍较狭,宽(3—)7—13(—25)mm,而四倍体的普遍较宽,宽(7—)15—34 mm,叶片宽度与地理分布也存在一定关系(图 5)。然而,新疆的二倍体柳兰的叶普遍较宽大(15—25 mm),这与欧洲的居群类似。
- 4. 叶柄 过去分类学家忽视了叶柄性状。 事实上不同倍性的柳兰叶柄长度 明显 不同,与地理分布也存在一定关系(图 5)。 二倍体柳兰的叶常无柄或仅具 1—2mm 长的短柄,而四倍体柳兰多少具柄,柄长 2—7 mm。
- 5. 花瓣大小 柳兰的花序长短和花瓣的形状与色泽深浅变异颇大。花瓣形状在新疆和西南地区的普遍较宽,而华北与东北地区的较狭,然而这同倍体水平无关。花瓣的大小,二倍体的偏小,长9—15(—19) mm,宽3—9(—11) mm,唯产新疆的普遍较大,同北欧的相似;四倍体的偏大,长14—25 mm,宽7—15 mm,这与地理分布也有一定关系(图 4)。

不同倍性同形态学与地理学之间的关系 本文采用了矩形散点图来表达形态学与地理学之间的关系。由于我国地广、多山、地形地貌复杂,仅用纬度或海拔高度分析同形态



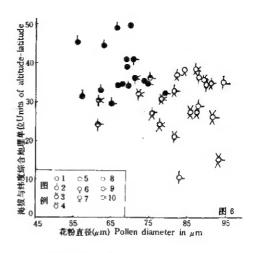


图 5 柳兰不同亚种的叶片与叶柄长度同地理分布关系。

Fig. 5 Scatter diagram, showing correlation between leaf characters and geography in different subspecies of E. angustifoilium.

黑点 solid circle = 柳兰 Subsp. angustifolium; 白圈 open circle = 毛脉柳兰 Subsp. circumvagum. 1—4.叶柄长度 (mm) petiole length (mm): 1. 0; 2. <2; 3. 2—5; 4. >5.

图 6 柳兰不同亚种的形态组合性状与地理分布关系

Fig. 6. Scatter diagram, showing correlation between a combination of characters and geography in different subspecies of *E. angustifolium*

黑点 solid circle = 柳兰 Subsp. angustifolium; 白圈 open circle = 毛脉柳兰 Subsp. circumvagum; 半黑圈 semi-solid circle = 中间型 intermediate.

1-4.200 粒花粉中含 4-5 孔的百分率% of 4-5-pored pollen of 200 grains: 1. 0-5%; 2. 6-30%; 3. 31-50%; 4. 50%. 5-7. 叶柄长度(mm) petiole length in mm: 5. 0; 6. 1-2; 7. >2.8-10. 叶片宽度(mm) leaf width in mm: 8. <15; 9. 15-22; 10. >22.

学性状间的相关性,很难做出准确的回答。因此,我们拟用一种纬度与海拔综合地理单位 (units of altitude-latitude) 作为地理学指标,以便定量化地与形态学性状作比较。即:综合地理单位—纬度单位十海拔高度单位。设1个纬度—1 纬度单位,海拔100m—1 海拔高度单位。再根据柳兰在中国分布的最南界大约为北纬25°,设25°N为零。这样,可根据每号标本采集地的纬度与海拔高度求出该标本的综合地理单位来。如采自四川峨眉山的方文培2822号标本,其纬度为29°5′N,纬度单位应为: 29.5—25—4.5,其海拔为2200 m,海拔高度单位为: 2200÷100—22,这样,该标本的综合地理单位应为:

$$4.5 + 22 = 26.5$$

我们在制作柳兰的形态与地理相关性的矩形散点图时,选用各地区倍性不同的柳兰各 20 号标本,以综合地理单位作纵坐标,以某一形态性状作横坐标,同时也可将有关性状在每一散点上用不同的方向表示出,这样从每一矩形图上可以显示出该种植物形态与地理的关系来。

从上述资料不难看出,不同倍性柳兰不仅在形态学上与花粉学上有区别,在地理分布上也不同,它们之间的相互关系在图 6 中清楚地表示出来。二倍体柳兰集中于坐标图的左上方,在地理上分布纬度较高,在西南低纬度山区常分布于高海拔地带,其综合地理单位

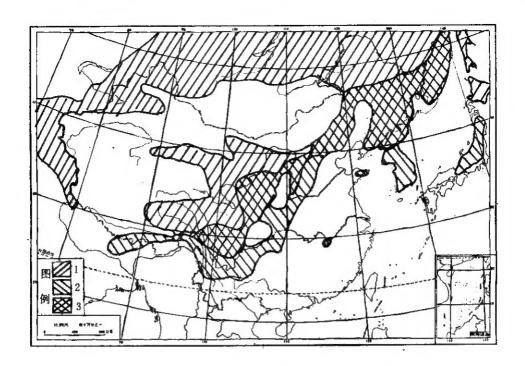


图 7 柳兰不同亚种在中国及其邻近地区的地理分布投影图。

Fig. 7. A distributional shadow map of different subspecies of E. angustifolium in China and the adjacent regions.

1.柳兰 subsp. angustifolium 2. 毛脉柳兰 subsp. circumvagum 3. 重叠区 overlapping area

为 30—50; 它在形态学上也与四倍体称兰不同(详见分类学部分)。而四倍体柳兰在图 6 中集中于坐标图的右下方;在地理上分布纬度较低,在西南山区常分布低海拔地带,其综合地理分布单位为 10—38。图 7 清楚地显示出二倍体与四倍体柳兰在地理分布上存在着一个宽阔的重叠区。在同区域内,不同倍体常分布于不同的海拔高度,在西南山区及喜马拉雅尤为明显,二倍体较四倍体分布得更高。在重叠区内两种倍性的柳兰在形态上也不难区别,有时出现中间过渡类型的个体,如采自云南中甸的冯国楣 2476 (KUN) 二倍体柳兰叶中脉背面无毛,但叶较宽(约 20 mm),边缘近平坦,花粉粒直径 61.29 μm, 4 孔和 5 孔花粉占 2%,败育率达 43%。 采自四川康定的 McLaren AC216 (PH) 四倍体柳兰叶宽仅 8—14 mm,背面中脉仅有很少柔毛,几无叶柄,花粉粒较小(径 77.8 μm), 3 孔达 96%,不育率达 56%。这两个倍性的柳兰种宗分布区不同,但存在着重叠区与过渡类型,这正是形态地理亚种所具有的重要特征。

分类学处理

1. 柳兰(种子植物名称)

Epilobiun angustifolium L., Sp. Pl. 347. 1753: Maxim., Prim. Fl. Amur. 471. 1859, pro parte; Hance in Journ. Bot. 1883: 321. 1883; Hausskn., Monogr. Epilob. 37. 1884, pro parte; Forb. et Hemsl. in Journ. Linn. Soc. Bot. 23: 307.

1887, pro parte; Ohwi, Fl. Jap. 820. 1953, pro parte; Raven in Bull. Brit. Mus. (Nat. Hist.) Bot. 2: 346. 1962, pro parte; Mosquin in Brittonia 18: 167. 1966; Hoch et Raven in Nasir et Ali, Fl. Pakistan 139: 11, f. 1, E-I. 1981, pro parte. [Type from Europe]—Chamaenerion angustifolium (L.) Scop., Fl. Carniol., ed. 2, 1: 271. 1772; Steinberg in Schischk. et Bobrov, Fl. URSS 15: 622, t. 27, f. 3. 1949, pro parte; T. N. Liou et al., Clav. Pl. Chin. Bor.-orient. 235, t. 74, f. 3. 1959 et Fl. Pl. Herb Chin. Bor.-orient. 6: 155, t. 61, f. 1—3. 1977, pro parte; C. J. Wu in H. C. Fu et al., Fl. Intramongol. 4: 129. t. 61. f. 1—3. 1979, pro parte; B. E. Grubov, Man. Vasc. Pl. Mongol. 185. 1982; H. Li in C. Y. Wu, Fl. Xizang. 3: 364. 1986, pro parte.—Epilobium spicatum Lam., Fl. Franc. 3: 482. 1778. [Type from France]—Chamerion angustifolium (L., em.) Holub. in Folia Geobot. Phytotax. 7: 86. 1972.

本种植物具有柳兰组 Sect. Chamaenerion 的特征: 叶螺旋状排列,花两侧对称,花管 (floral tube 或 hypanthium) 缺,花瓣全缘,雄蕊排成一轮,花粉粒以单个散落,花柱受粉前弯曲,柱头 4 裂,花盘发达。

本种植物同产横断山与东喜马拉雅的网脉柳兰 E. conspersum Hausskn. 近似,其不同在于总状花序由多数花组成,花在芽时下垂,开花时变直立和叶无网状细脉等。

2. 柳兰(亚种)

E. angustifolium L. Subsp. angustifolium

茎高 20-130 cm 无毛。叶条形,长(3-)7-14(-18.5) cm,宽(0.3-)0.7-1.3(-2.5) cm,基部钝或近圆形,边缘全缘,常反卷,两面无毛;叶柄缺或长仅 1-2 mm。 花序长 5-40 cm,无毛。 花瓣长 9-15(-19) mm,宽 3-9(-11) mm; 花粉直径平均 68.43 (56.2-79.7) μ m,常具 3 孔。 n=18。

分布于欧亚大陆 (30一)40—70°N, 北美 50—70°N 之间温带地区及亚 热 带 高 山 地 带;在中国产黑龙江、吉林、辽宁西部、内蒙古、河北北部、山西北部、宁夏、甘肃、 青海、 新 疆、四川西部、 云南西北部及西藏北部及东部(图 7);生于华北地区海拔 (100—)500—2800 m, 西北地区海拔 1500—3500 m 和西南地区 2900—4700 m 山区森林开旷地、林缘、 火烧迹地、伐木地、砾石坡地向阳或半向阳环境,常成片生长。

检查过的标本:略(见参考文献[8])。

Representative specimens examined: See the present authors (refs. 8),

3. 毛脉柳兰 新拟

E angustifolium L. Subsp. circumvagum Mosquin in Brittonia 18: 167. 1966. [Type from Colorado, U. S. A.]—E. angustifolium L. f. pubescens Hausskn., Monogr. Epilob. 38. 1884.—Chamaenerion angustifolium (L.) Scop. var. platyphyllum Daniels, Fl. Boulder Colo. 176. 1911. [Type from Colorado, U. S. A]—Epilobium angustifolium L. var. platyphyllum (Daniels) Fern. in Rhodora 20: 5 1918.—Chamaenerion angustifloium auct. non (L.) Scop.: Hand.-Mazz., Symb. Sin. 7(3): 602. 1933; Steinberg in Schischk. et Bobrov, Fl. URSS 15: 622. 1949, quoad pl. Ussuri

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茎高 30-250 cm, 上部多少被柔毛。叶椭圆状披针形或条形,长 (6-)9-23 cm, 宽 (0.7-)1.5-3.4 cm, 基部常楔形,边缘平坦,疏生腺点状齿,背面中脉被短柔毛;叶柄长 2-7 mm。花序长 10-15 cm, 花序轴多少被柔毛。 花瓣长 14-25 mm, 宽 7-15 mm;花粉直径平均 85.68(75.6-94.8) μ m,除具 3 孔外,常混有较多的 4 或 5 孔。 n=36。

分布于亚洲的日本(本州)、朝鲜、苏联堪察加南部、萨哈林岛(库页岛)、远东地区及高加索地区、缅甸北部、喜马拉雅、巴基斯坦、土耳其,在欧洲只零星出现于欧洲西部,也普遍分于加拿大南部和美国北部与西部地区以及阿拉斯加湾的科迪亚克岛;在中国产黑龙江东部、吉林东部、辽宁、内蒙古东部、河北、山西、山东东部、河南西部、陕西、宁夏、甘肃东南部、青海东部、江西(庐山)、湖北西部、四川、贵州、云南与西藏东南部(图7);生于中国北部海拔(100—)500—1700(—2800) m 和西南部海拔(550—)1100—3100(—4350) m 的山区,生境同柳兰。

检查过的标本:略(见参考文献[8])。

Representative specimens examined: See the present authors(refs. 8),

毛脉柳兰 Subsp. circumvagum 是 Mosquin 根据一个变种名 Chamaenerion angustifolium var. platyphyllum Daniels 建立的,以该变种的模式 (美国,Colorado,Daniels 268, MSC) 为他的新亚种模式。诚然,Mosquin 在亚种等级上可以取新名,然而,他的新亚种既然是根据 Daniels 的一个变种名称建立的,那末他的新亚种名称最好采用 platyphyllum 新组合形式处理,遗憾的是他没有这样做。我们认为 Mosquin 对毛脉柳兰的命名法是不能效法的。

讨 论

- 1. 分布于北半球温带的广布种柳兰由 Mosquin (1966) 分成二倍体 (Subsp. angustifolium) 与多倍体 (Subsp. circumvagum) 两个不同亚种。 我们着重对分布于中国的 柳兰植物进行了研究,证明二倍体与四倍体柳兰在形态学、花粉学性状不同,分布区也不同,在重叠区内存在一些中间类型。因此,对不同倍性染色体柳兰种宗处理作两个亚种是很自然的。在中国至今还未发现六倍体,这有待今后进一步研究。
- 2. 柳兰的形态学性状差异显然主要是染色体的倍性不同决定的。在高等植物中以多倍化形式进行演化,柳兰是一个例子。倍性不同的柳兰亚种在形态学上除 Mosquin(1966)观察到的花粉直径与孔数、叶背面中脉毛被及叶片宽度四个性状外,还有叶片基部形态、叶缘、花序轴毛被与花瓣大小等共9个性状明显不同,在我们的矩形图中,不同性状指标把二倍体与四倍体柳兰划分成二个类群。然而我们的图表数据也显示出倍性不同柳兰的形态变异具有逐渐量变性质,正如 Mosquin(1966)指出的: 所研究的每种形态学特征的遗传似乎是由数量因子决定的,染色体每次加倍的结果部分地扩大了数量范围。有时环境饰变也是引起形态变异的一个不可忽视的因素。

- 3. 柳兰的地理学是很有趣的。二倍体与四倍体柳兰二亚种的分布在美洲基本上以北纬50°为界,界线较明显,重叠区较狭小。在欧洲几乎柳兰全为二倍体,只在阿尔卑斯山局部与高加索山脉混生有四倍体。然而柳兰在亚洲的分布则复杂得多,二倍体与四倍体柳兰2亚种在堪察加半岛、日本、朝鲜、远东、中国的大小兴安岭、长白山、经太行山与贺兰山至西南横断山区与东喜马拉雅地区混生形成大片的重叠过渡地带(见图7),在形态上的过渡类型也有发现,这就增添了在这过渡地带识别他们的难度。在亚洲东部形成这样广大过渡地带的原因,可能主要是这一地区的山多、山高、地形地貌复杂引起的。在横断山及东喜马拉雅山区,二倍体柳兰常分布在高海拔地带,而多倍体柳兰则常分布在低海拔地带。以上,也许是过去分类学家长期未能承认欧亚大陆两个柳兰亚种的主要原因。
- 4.二倍体柳兰分布于高纬度,甚至沿着北极常年结冰线也生长发育得很好(Mosquin, 1966),有时也分布干较低纬度(28°N以北)的高海拔山区;而多倍体柳兰仅见于相对较低纬度或较低的海拔地带。柳兰的细胞地理学资料表明柳兰可能起源于温带,而多倍体柳兰很可能是二倍体柳兰向南迁移遇到温暖气候染色体自我加倍的结果。

柳兰在喜马拉雅的细胞地理学也颇有趣(图 7)。 西喜马拉雅 (79°E 以西) 只分布有二倍体柳兰,这与中亚和天山情况一致,而东喜马拉雅 (87°E 以东) 主要为四倍体柳兰,只在最东段的高海拔地带才有二倍体柳兰分布,而在中喜马拉雅 (80—87°E) 却无柳兰分布,这说明喜马拉雅的这种植物很可能是从东部和西部方向分别地进入这个地区的。

- 5.多倍体毛脉柳兰 (Subsp. circumvagum) 间断地分布至华东庐山和山东东部的昆俞山(图7)。有趣的是 1935 年在江西庐山的金牛山记录到毛脉柳兰(熊跃国 113,LBG),之后无论在庐山还是附近省区再没有记录过这种植物。这种间断分布式样在其他温带成分植物中也偶尔可见,如支柱蓼 Polygonum suffultum Maxim.,尼泊尔酸模 Rumex nepelensis Spreng,散生栒子 Cotoneaster divaricatus Rehd. et Wils. 等。 这种岛状分布,可能是过去(至少在第四纪)冰期植物南迁,冰后期分布区又向北收缩,在东南部山地留下的残遗分布。 也可能是晚第三纪喜马拉雅造山运动(吴征镒等,1983)、在第四纪华东地区严重受到冰川侵袭,以及这些低山地区人为活动频繁影响所致。
- 6.广布种多数包含有多个分类群,柳兰便是一例。然而有的广布种表现为单型,如柳叶菜 (E. hirsutum L.) (见参考文献 [8])。

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VARIATION PATTERNS AND SYSTEMATICS OF THE WIDESPREAD SPECIES EPILOBIUM ANGUSTIFOLIUM L. (ONAGRACEAE) IN CHINA

CHEN CHIA-JUI

(Institute of Botany, Academia Sinica, Beijing)

PETER C. HOCH AND PETER H. RAVEN

(Missouri Botanical Garden, St. Louis, Missouri, USA)

Abstract Cytological, morphological, and geographical studies of *Epilobium angustifolium* in China reveal two partly distinct, partly overlapping entities that are best treated as subspecies. The diploid (n=18) subsp. angustifolium has smaller, triporate pollen grains, typically glabrous stems and leaves, and smaller leaves and flowers, and occurs in colder, more northern areas, and at higher elevations in overlap zones. The tetraploid (n=36) subsp. circumvagum has larger pollen with a mixture of quadriporate pollen grains, pubescent stems and leaves, and larger leaves and flowers, and occurs in warmer parts of southern China and at lower elevations. We report 11 chromosome counts, six diploid and five tetraploid, including the first reported tetraploids in Asia.

Key words China; Epilogium angustifolium; Complex; Variation patterns; Cytology; Systematics; Geography

INTRODUCTION

Epilobium angustifolium L. is a widespread and variable circumboreal species, found over

much of boreal and montane North America and Eurasia. Many infraspecific taxa have been proposed, based on the great morphological variability, and cytological studies have revealed the presence of three ploidy levels in the species, n=18, 36, and 54 (Mulligan 1957; Löve & Löve 1961; Mosquin 1963, 1966a, 1966b; Raven & Moore 1964). Mosquin (1966a) proposed a taxonomy for E. angustifolium that distinguished diploid (n=18) subsp. angustifolium from polyploid (n=36, 54) subsp. circumvagum Mosquin based on a combination of leaf, pollen, and pubescence characters. This taxonomy worked well in Europe (where there are no polyploids) and North America, but there were too few chromosome counts from Asia to assess its utillity there. In recent Asian treatments, Raven (1968), Hoch & Raven (1981), and H. Li (1986) treated this species Without infraspecific taxa, as done by most Chinese botanists (refs.. 1—5), as Chamaenerion angustifolium (L.) Scop.

As part of our monographic study of *Epilobium* in China (refs. 8). we undertook studies of cytology, morphology, and geography of *E. angustifolium* in order to test the validity of Mosquin's taxonomy in Asia.

RESULTS AND OBSERVATIONS

For this study, we examined more than 1,500 herbarium specimens from China and adjacent regions, and did field work in Hebei, Sichuan, Gansu, and Xinjiang Provinces.

Cytology: Mitotic chromosome counts were obtained from root-tips of greenhouse-grown plants, and meiotic counts from field-collected buds. All materials were fixed in 1:3 acetic-alcohol, stored in 70% ethanol at 0° to -10° C, hydrolyzed in 1N HCl at 60° C for 2 minutes, and squashed in aceto-orcein. We here report chromosome counts from 11 populations in China (Table 1), six of which are diploid and five tetraploid; there were no hexaploids. These counts are the first known to us from China, and the first tetraploid reports from Asia.

Morphology: We selected 54 collections from herbaria throughout China for intensive study, and designated them as subsp. angustifolium or circumvagum based on their overall morphology (Tables 2—3), as delimited by Mosquin (1966a).

Pollen characters: To measure pollen grain diameter, pore number, and fertility, pollen from mature buds was mounted on slides and examined with malachite green-acid fuchsin-orange G stain (Alexander 1969). The average size of fertile grains was greater in subsp. circumvagum (85.7 μm) than in subsp. angustifolium (68.4 μm), although the size ranges overlap (Fig. 1). Also, 70% (24/34) of the samples of subsp. circumvagum had >5% 4—5-porate grains, whereas only 5% (1/20) of the samples of subsp. angustifolium had >5% 4—5-porate grains; in most samples, the majority of the grains are 3-porate. These results are comparable to those of Mosquin (1966a) in North America, but his samples showed greater pollen size overlap between the subspecies.

Many collections had some sterile pollen (Tables 2, 3), and we found completely (Xizang, Zhangmu, Y. T. Chang & K. Y. Lang 651, PE) or nearly completely (Sichuan, Emei-shan, Y. Chen 7133, NAS) sterile collections. This infertility might be genetic or environmental.

Pubescence: Plants of *Epilobium angustifolium* have glabrous to densely strigillose abaxial leaf midribs and upper stems. Despite rather continuous variation in hairiness, glabrous plants tend to have small pollen grains, and pubescent plants larger grains (Fig. 2). Mosquin

(1966a) used this difference in pubescence as a primary character for distinguishing subsp. angustifolium (always glabrous) from subsp. circumvagum (glabrous to pubescent).

Leaf characters: Plants with glabrous leaf midribs and smaller pollen grains (subsp. angustifolium) also have leaves with subrounded or obtuse bases and entire, subrevolute margins, whereas plants with strigillose midribs and larger pollen (subsp. circumvagum) have cuneate bases and subdenticulate, flat margins. The shape of the leaf base is, in fact, a reliable character for distinguishing the two subspecies. The length of the petioles also differs between subsp. angustifolium (sessile to 1—2 mm long) and subsp. circumvagum (2—7 mm long; Fig. 5).

Mosquin (1966a) used differences in leaf width to separate the taxa, and in the Chinese material, leaves of subsp. angustifolium are (3—)7—13(—25) mm wide, those of subsp. circumvagum (7—)15—34 mm wide. Although leaf width generally increases at lower latitudes and altitudes (Fig. 5), there is much local variation. For example, most plants from the Altay-Tianshan region of western China have broad leaves (13—25 mm wide) even though they appear on other grounds to be entirely diploid.

Petal size: The two taxa differ modally in this character, but their ranges overlap (Fig. 4): subsp. angustifolium has petals 9—15(—19)×3—9(—11) mm, whereas those of subsp. circumvagum are 14—25×7—15 mm.

Geography and ecology: The topographic complexity in eastern Asia and the broad ranges of the two subspecies obscures the relationship between geography and morphology. By using a combined measure of altitude and latitude, based on the approximate equivalency in ecological zonation between movement through 1 degree of latitude away from the equator with a rise of 100 m in elevation, we can demonstrate correlations between this ecogeographic measure with pollen diameter and pore number (Fig. 2), petal area and leaf pubescence (Fig. 4), leaf width and petiole length (Fig. 5), and a combination of them (Fig. 6).

TAXONOMY

The differences in ploidy level, correlated with the partly discrete, partly overlapping morphological differences, leads us to recognize two subspecies in *Epilobium angustifolium* in China, in agreement with the delimitation of Mosquin (1966a), as follows:

Epilobium angustifolium L. subsp. angustifolium

Stems 20—130 cm tall, subglabrous. Leaves (3—)7—13(—25) mm wide, glabrous, with obtuse or subrounded base, entire and often revolute margin; petioles lacking or 1—2 mm long. Petals 9—15(—19) mm long, 3—9(—11) mm wide; pollen usually triporate, less than 80 µm in diameter. Gametic chromosome number, n=18.

Distribution (Fig. 7): Widespread from (30°—) 40° to 70° N in Eurasia, and from 50° to 70° N in North America; in China occurring in Heilongjiang, Jilin, western Liaoning, Nei Monggol, Hebei. Shanxi, Ningxia, Gansu. Qinghai, Xinjiang, Western Sichuan, northwestern Yunnan, and northern and eastern Xizang (Tibet), at elevations 100—)500—2800 m in northern China, 1500—3500 m in north-western China, and 2900—4700 m in south-western China.

Epilobium angustifolium L., subsp. circumvagum Mosquin

Stems 30—250 cm tall, often strigillose alove. Leaves (7-)15-34 mm wide, with strigillose abaxial midrib, cuneate base, denticulate and flat margin; petioles 2—7 mm long. Petals 14—25 mm long, 7—15 mm wide; pollen a mixture of triporate and quadri- or quinque-porate grains, mostly more than 80 μ m in diameter. Gametic chromosome number, n=36.

Distribution (Fig. 7): Widespread from 25° to 50° N in Eurasia, and from 35° to 55° N in North America; in China, occurring in eastern Heilongjiang, eastern Jilin, Liaoning, eastern Nei Mongol, Hebei, Shanxi, Shandong (Mt. Kunyu), western Henan, Shaanxi, Ningxia, south-eastern Gansu, eastern Qinghai, Jiangxi (Mt. Lushan), western Hubei, Sichuan, western Guizhou, north-eastern to western Yunnan, and eastern to southern Xizang; at elevations (100—)500—1700(—2800) m in northern China and (550—)1100—3100(—4350) m in southwestern China.

Notes: In establishing this taxon, Mosquin (1966a) wrote "Epilobium angustifolium subsp. circumvagum Mosquin, subsp. nov.", even though he based it on a previous valid name, Chamaenerion angustifolium var. platyphyllum Daniels. and indicaded the type of var. platyphyllum (Colorado, Daniels 268, MSC) as the type of his new taxon. He was free to use a new basionym at the subspecific level. Mosquin, however, did not treat platyphyllum as the name of his new taxon (a new combination), but gave a new name. His treatment of the nomenclature of subsp. circumvagum should not be an example to be followed.

DISCUSSION

Careful study of Epilobium angustifolium in China shows that the characters used by Mosquin (1966a) to delimit the subspecies, particularly pollen size (Figs. 2, 6), also differentiate two entities in China. Leaf base shape and petiole length (Fig. 5) are also useful, as to a less degree are leaf margin, upper stem pubescence, and petal area. Correlation of these morphological characters with differences in ploidy level (Table 1) supports recognition of the subspecific status of these two entities.

The morphological differences between th two subspecies are mostly quantitative, and intermediate populations occur, further indicating that the subspecific rank is appropriate for these taxa. Mosquin (1966b, 1967) found cytogenetic and other evidence that the tetraploids are autopolyploids, and the pattern in China supports this hypothesis.

Despite the complex distributional pattern of the two subspecies in China (Fig. 7), the basic pattern of diploids in higher, more northern habitats and tetraploids in lower, more southern areas is the same as in North America.

One collection of subsp. circumvagum (Mt. Lushan, Jiangxi, 1935, Y. G. Xiong 113, LBG), is highly disjunct in eastern China; this pattern is also seen in other taxa, such as Polygonum suffultum Maxim., Rumex nepalensis Spreng. (Polygonaceae), and Cotoneaster divaricatus Rehd. & Wils. (Rosaceae). This island-pattern distribution might be a remaining trace of the populations of E. angustifolium in the southern part after the populations had retreated northwards with the regression of glacier in the Quaternary. The subsidence of eastern China accompanied the uplift of the Himalayan region (Wu & Wang 1983), and gradual warming in the east forced cold-adapted floras north and west, leaving relicts in scattered higher places (Lushan), where they have been further depleted by recent human disturbance.